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PERICARP STUDIES IN MAIZE. I. THE INHERITANCE OF PERICARP COLORS[1]

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INTRODUCTION

The inheritance of pericarp color has been studied by many workers with maize. The ordinary red pericarp has been found to be a simple dominant to colorless pericarp. EMERSON (1921), in his studies on general plant colors of maize, found that the red color was modified to brown by one of the recessive plant color factors. The factorial relations are as follows:

$$P\ A = \text{red}$$
$$P\ a = \text{brown}$$
$$p\ A = \text{colorless}$$
$$p\ a = \text{colorless}$$

A series of pericarp types including red, variegated, red-cob white, orange and others, behave essentially as a series of allelomorphs.

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Another type of pericarp color is a red or purple color frequently found among the Indian maize of the West and Southwest. This type we have called cherry. In inheritance it has been found to be independent of red and related types. It occurs only on purple and dilute-purple plants. It is also modified to a brownish by the recessive *a* factor.

In addition to the above, there are several pericarp colors which are not yet analyzed, such as the sun-red color of many varieties, and some of the pericarp colors found in South American varieties of maize.

The present paper deals with data bearing on the factor relations involved in pericarp-color inheritance. It is to be followed by papers on the allelomorphism of the red pericarp series and on the mutability of the factor for variegated pericarp.

NOMENCLATURE

For the convenience of the reader, the factors and symbols used in this paper are given in the following list:

$P\ p$, members of a series of allelomorphic or closely linked factors for red, variegated, red-cob white and other pericarp colors and color patterns.

r^{ch}, one member of an allelomorphic series of factors affecting aleurone and general plant colors. This allelomorph is necessary for the production of cherry pericarp color.

R^r, R^g, r^r, r^g, other members of the same series. None of these produce cherry pericarp color.

$A\ a$, $B\ b$, $P_l\ p_l$, general plant-color factors, interacting in the following manner (EMERSON 1921):

$A\ B\ P_l$, purple
$A\ B\ p_l$, sun-red
$A\ b\ P_l$, dilute purple
$A\ b\ p_l$, dilute sun-red
$a\ B\ P_l$, brown
$a\ B\ p_l$, green
$a\ b\ P_l$, green
$a\ b\ p_l$, green

PIGMENTS PRESENT IN COLORED PERICARP

The red pericarp color is produced by a pigment which is almost insoluble in water, alcohol, benzene and similar solvents, but which dissolves in hot dilute sulfuric acid. Thin sections[2] of pericarp (15 to 25μ)

[2] Microscopic sections have been prepared as outlined in a previous paper (ANDERSON 1921).

are orange-red, or brick-red, in color. The brick-red pigment is characteristic also of variegated, orange, and the other pericarp color types of the same series. Brown pericarp has this pigment replaced by a yellowish one.

Cherry color is produced by a water-soluble purplish pigment, probably the same as that found in the sheaths and leaves of purple plants. It is probably an extension of the same pigment into the pericarp. Cherry is found only on purple or dilute-purple plants. The brownish pericarp color appears likewise to correspond to the brown plant color which SANDO and BARTLETT (1922) have shown to be due to the flavonol, quercetrin, or its glucoside, isoquercitrin.

TABLE 1

Back-crosses of A p × a P with a p.

PEDIGREE NUMBERS	PARENT TYPES		RECOMBINATIONS		TOTAL
	A p	*a P*	*A P*	*a p*	
E1494	25	35	31	38	129
E1497	17	22	21	24	84
E1514	22	30	40	28	120
E2019	22	31	23	37	113
E2021	35	28	31	29	123
E2074	7	10	15	9	41
E2099	8	7	6	2	23
E5105	13	15	13	7	48
E7288	28	32	29	28	117
E9084	24	26	37	23	120
E9085	32	38	36	35	141
Sub-total	233	274	282	260	
Total	507		542		1049

FACTOR RELATIONS OF PERICARP COLORS

In the following pages, data are presented bearing on the inheritance of red and cherry pericarp color, the interaction of factors for pericarp color, the independence of the factors for red and cherry, and the relation of these factors to other factors affecting pericarp color. The data presented are selected, partly for simplicity, and partly for their value in the study of the linkage relations of Mendelian factors of maize.

Factor relations of red pericarp, P

Relation to *A*

Crosses of green plants having brown pericarp, *a P*, with dilute-sun-red plants having colorless pericarp, *A p*, have given in F_1 dilute-sun-red plants with red pericarp. The F_2 has given red, brown, and white (colorless) pericarp, red occurring on dilute-sun-red plants only, brown on green plants only, and white on both plant-color types. Similar crosses in which one parent had brown pericarp and the other had orange, variegated red, or white-capped red pericarp, have given similar results. The data from back-crosses of these F_1's with the double recessive, *a p*, are given in table 1.

A single F_1 of $A\ P \times a\ p$ back-crossed with *a p* (pedigree E7291) gave 26 *A P*, 24 *A p*, 25 *a P*, and 27 *a p*. Of the 1151 plants of the twelve back-cross progenies, 560 had the parental combinations of plant and pericarp colors while 591 had recombinations of these characters, a recombination percent of 51.3 ± 1.0. This indicates that the factors *A* and *P* are independent (not linked) in inheritance.

Relation to P_l

The plant-color factor P_l has no influence on the production of red pericarp color. Data from back-crosses of F_1 plants with the double recessive are given in tables 2 and 3. Crosses each parent of which had one dominant and one recessive factor are listed in table 2.

Crosses one parent of which had the dominant factors and the other the two recessive ones are given in table 3.

TABLE 2

Back-crosses of $P_l\ p \times p_l\ P$ with $p_l\ p$.

PEDIGREE NUMBERS	PARENT TYPES		RECOMBINATIONS		TOTAL
	$P_l\ p$	$p_l\ P$	$P_l\ P$	$p_l\ p$	
A238	47	59	45	57	208
A241	32	28	31	37	128
A243	15	17	13	12	57
A248	33	41	32	42	148
A249	45	40	39	55	179
A250	47	23	36	28	134
E1514	10	22	17	12	61
E1564	5	1	4	7	17
E2019	16	10	13	6	45
E2021	24	16	15	10	65
E7297	29	23	25	21	98
E9094	25	25	25	32	107
Sub-total	328	305	295	319	
Total	633		614		1247

The percent of recombination for the data in table 2 is 49.2 ± 1.0 and for those in table 3 is 49.4 ± 1.2, thus indicating independent inheritance of P_l and P.

Relation to R

Crosses involving red pericarp and the aleurone-color factor R, back-crossed to the double recessive (white-pericarp "R tester," $p\ A\ C\ r$) have given the results recorded in table 4.

The recombination percent, 50.9 ± 1.1, indicates that P and R are inherited independently.

Linkages of P

KEMPTON (1921) has reported linkage between the factors for red pericarp and brachytic culms. The percent of crossing over found was

TABLE 3

Back-crosses of $P_l\ P \times p_l\ p$ with $p_l\ p$.

PEDIGREE NUMBERS	PARENT TYPES		RECOMBINATIONS		TOTAL
	$P_l\ P$	$p_l\ p$	$P_l\ p$	$p_l\ P$	
A511	55	57	62	47	221
A529	96	111	81	96	384
A654	31	47	42	61	195
E5105	9	5	8	4	26
Sub-total	191	220	193	208	
Total	411		401		812

TABLE 4

Back-crosses of $R\ p \times r\ P$ with $r\ p$.

PEDIGREE NUMBERS	PARENT TYPES		RECOMBINATIONS		TOTAL
	$R\ p$	$r\ P$	$R\ P$	$r\ p$	
A1819	91	77	67	92	327
A1825	38	38	43	48	167
E7297	21	21	38	18	98
E7299	21	17	22	19	79
E7301	52	38	44	43	177
E7345	8	13	8	7	36
E9098	31	21	26	30	108
Sub-total	262	225	248	257	
Total	487		505		992

about 37. EMERSON (1920) has reported a close linkage of red pericarp color with tassel seed. Larger numbers have since been grown. There is about one percent of crossing over. Linkage of red pericarp with fine-striped leaf has also been found. The percent of crossing over is about 35. The data concerning this linkage are to be published in a later paper.

Factor relations of cherry pericarp

Relation to *R*

Crosses of cherry pericarp with purple aleurone (*A C R*) have been back-crossed to *R*-testers (*A C r*). The F_1 could not be used as the pistillate parent of the back-cross, as cherry pericarp obscures the aleurone color.

TABLE 5

Back-crosses of cherry pericarp, r^{ch} × purple aleurone, R, with white-pericarp R-testers, A C r.

PEDIGREE NUMBERS	PURPLE SEEDS		WHITE SEEDS	
	Cherry pericarp	White pericarp	Cherry pericarp	White pericarp
A 204	0	9	8	0
A 276	0	14	7	0
A 280	0	47	45	0
A 452	0	29	22	0
A 711	0	35	28	1
A 713	0	7	5	0
A 715	1	83	96	1
A 717	1	243	227	3
A 719	1	141	129	2
A1778	1	77	68	0
A1784	1	63	41	1
Total	5	748	676	8

When the reciprocal back-cross was made, the dominant *R* being brought in by the pollen only, the resulting seeds were mottled, as described by EMERSON (1918) and KEMPTON (1919). These mottled seeds were frequently very light and perhaps even entirely white, making the classification of aleurone color not entirely satisfactory. The distributions are given in table 5. All cultures throwing sun-red or dilute-sun-red plants were discarded, as cherry pericarp occurs only on purple and dilute-purple plants.

In general the purple seeds gave only white pericarp and the white seeds gave only cherry. Thirteen exceptions were recorded from a total of 1437 back-cross plants. Progenies grown from open-pollinated ears of the cherry exceptions gave no evidence of any recombination or crossing over having occurred. All of the exceptions were probably due to the difficulty of classifying the seed with respect to aleurone color.

The test was repeated, making use of the effect of the R factor on plant and anther color as well as on aleurone color. The results are given in table 6.

TABLE 6

Back-crosses of cherry pericarp, r^{ch} × purple aleurone, R^g, with white-pericarp R-testers, A C r^g.

PEDIGREE NUMBERS	PURPLE SEEDS		WHITE SEEDS	
	Dilute-purple plants, cherry pericarp	Green plants, white pericarp	Dilute-purple plants, cherry pericarp	Green plants, white pericarp
A1786	1	69	63	7
A1790	1	69	64	3
A1794	0	13	9	0
A1796	1	61	74	6
A1804	1	40	39	0
Total	4	252	249	16

The ears failed to mature as well as in the previous test, and aleurone color classification was more difficult. Twenty exceptions were recorded from a total of 521 plants. There were no recombinations of plant color and pericarp color. Of the four cherry exceptions, two were selfed and gave only colorless aleurone. Of the sixteen white-pericarp exceptions, twelve were selfed or crossed with R testers. All were heterozygous for aleurone color. Three others had open-pollinated ears throwing a large percentage of colored seeds. One plant failed to produce a good ear. Thus, of a total of twenty apparent exceptions, fourteen were proven not to be recombinations of aleurone and pericarp color, and three more gave strong indications of not being. The three untested plants were probably not different from those tested.

As indicated above, recombinations of cherry pericarp with aleurone and plant color (R factor) probably do not occur. We, therefore, assume that the factor responsible for cherry pericarp is one member of the allelomorphic series R^r, R^g, r^r, r^g for plant and aleurone color. This allelomorph we designate by the symbol r^{ch}.

Relation to P_l

Crosses of cherry pericarp with sun-red or dilute-sun-red plants give progenies which, in the F_2, segregate for both plant and pericarp colors.

Among the purple and dilute-purple plants, cherry and white pericarps occur in ratios approximating 3 to 1. All the sun-red and dilute-sun-red plants have white pericarp. In a back-cross (A721) to the double recessive the following numbers of individuals of the indicated color types were obtained:

Dilute-purple plants with cherry pericarp	84
Dilute-purple plants with white pericarp	95
Dilute-sun-red plants with white pericarp	174

TABLE 7

Back-crosses of $R\ P_l \times r\ p_l$ with R-testers, $A\ C\ r\ p_l$.

PEDIGREE NUMBERS	PARENT TYPES		RECOMBINATIONS		TOTAL
	$R\ P_l$	$r\ p_l$	$R\ p_l$	$r\ P_l$	
E1555	14	17	18	28	77
E1557	14	14	15	15	58
E1561	5	9	10	13	37
E1570	13	12	9	12	46
E1572	9	9	6	12	36
E1575	24	24	24	24	96
E5301	16	16	19	16	67
E7297	32	24	37	16	117
E7299	22	23	33	35	113
E7344	13	20	8	19	60
E8259	10	10	15	8	43
Sub-total	172	178	194	198	
Total	350		392		742

Since r^{ch} is one of the multiple allelomorphs of the R series, linkage or independent inheritance of r^{ch} and P_l can be determined from crosses involving $P_l\ p_l$ and the aleurone factor pair $R\ r$. Data from back-crosses of $R\ P_l \times r\ p_l$ with $r\ p_l$ are given in table 7 and of $R\ p_l \times r\ P_l$ with $r\ p_l$ in table 8.

The records of table 7 give 52.8 ± 1.2 percent, those of table 8 give 47.9 ± 1.9 percent, and those of the two combined give 51.2 ± 1.0 percent of recombination. Obviously r^{ch} is inherited independently of P_l.

Relation to *A*

The relation of cherry pericarp to the A factor may be illustrated by culture A93 obtained by selfing a dilute purple plant with cherry pericarp. This culture gave six dilute-purple plants with cherry pericarp and one green plant with "brownish" pericarp. The latter bred true and when crossed with dilute-sun-red gave only dilute-purple plants with cherry pericarp. Its constitution must have been $a\ a\ P_l\ P_l\ r^{ch}\ r^{ch}$. One of its dilute-purple sibs selfed gave 22 dilute-purple plants with cherry pericarp and 10 green plants with brownish pericarp. Other cultures have given two types of green plants, the one type with brownish pericarp, the other with white. Tests of these have shown the brownish-pericarp plants to be of the constitution $a\ P_l\ r^{ch}$, and the white-pericarp plants to be lacking either dominant P_l or the cherry allelomorph of R.

TABLE 8

Back-crosses of $R\ p_l \times r\ P_l$ with R-testers, $A\ C\ r\ p_l$.

PEDIGREE NUMBERS	PARENT TYPES		RECOMBINATIONS		TOTAL
	$R\ p_l$	$r\ P_l$	$R\ P_l$	$r\ p_l$	
E8261	30	41	30	31	132
E8263	17	22	15	20	74
E8723B	2	7	8	10	27
E8725	15	10	15	10	50
E8729	14	11	11	12	48
Sub-total	78	91	79	83	
Total	179		162		341

The three factors concerned here are independent in inheritance. The independence of R and P_l has been shown above (tables 7 and 8). That factors A and R and factors A and P_l are inherited independently has been shown by EMERSON (1918, 1921).

The relation of these factors to plant and pericarp colors is as follows:

	Pericarp color	*Plant color*
$A\ P_l\ r^{ch}$	Cherry	Purple or dilute purple
$A\ P_l\ r^r$	White	Purple or dilute purple
$A\ p_l\ r^{ch}$	White	Sun-red or dilute sun-red
$A\ p_l\ r^r$	White	Sun-red or dilute sun-red
$a\ P_l\ r^{ch}$	Brownish	Brown or green
$a\ P_l\ r^r$	White	Brown or green
$a\ p_l\ r^{ch}$	White	Green
$a\ p_l\ r^r$	White	Green

DISCUSSION AND SUMMARY

The pericarp colors which are of most frequent occurrence in North American maize can be divided into two strikingly different categories:

1. A series of allelomorphic or closely linked types characterized by a rather insoluble brick-red or orange-red pigment. These types differ among themselves chiefly in the amount and distribution of this pigment. The brick-red pigment is replaced by a yellowish one when the factor a is homozygous, the distribution and relative intensity remaining the same. The red pericarp pigment develops on sun-red, dilute-sun-red, purple and dilute-purple plants, and the brown pericarp pigment on brown and green plants. The characteristic factor P is independent of A, R, and P_l and is linked with the factors for brachytic culm, tassel seed, and fine-striped leaf.

2. Cherry pericarp color, due to the presence in the pericarp of the water-soluble purple pigment (anthocyanin) found commonly in the sheaths, leaves, anthers, aleurone, etc. Its development is determined by two dominant factors, the factor r^{ch} and the purpling factor P_l for plant color. The purple pigment is replaced by a yellowish pigment when the factor a is homozygous. Since dominant P_l is required for the production of cherry pericarp color, it cannot occur on sun-red or dilute-sun-red plants. The factor r^{ch} is one member of the R series of allelomorphs for aleurone and plant color and is consequently linked with the factors for golden leaf and luteus seedlings. It is independent of P, P_l, and A. The factor P_l is independent of R, P, and A, and is linked with the factors for yellow endosperm and salmon silks.

The interaction of factors in the production of pericarp color in the two series may be represented thus:

Red series:

$P\ A$	red
$P\ a$	brown
$p\ A$	white
$p\ a$	white

Cherry series:

$r^{ch}\ P_l\ A$	cherry
$r^{ch}\ P_l\ a$	brownish
$r^{ch}\ p_l\ A$	white
$r^{ch}\ p_l\ a$	white

Other allelomorphs of the R series give white pericarp only.

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